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Response of soil respiration and its components to experimental warming and water addition in a temperate Sitka spruce forest ecosystem

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ABSTRACT

Future climate change is expected to alter the terrestrial carbon cycle through its impact on soil respiration. In this study, we determined the responses of soil respiration and its components to experimental warming with or without water addition. A replicated *in situ* heating (~2 °C above ambient soil temperatures) and water addition (170 mm in total each year) experiment was carried out for the first time in a temperate plantation forest of Sitka spruce over the period 2014–2016. R_h was measured inside deep collars (35 cm deep) that excluded root growth, while R_s was measured using the static chamber approach and near-surface collars (5 cm deep) and R_a calculated by subtracting R_h from total soil respiration (R_s). Experimental warming significantly increased R_s, R_h and R_h/R_s, but had no effect on R_a. In contrast, none of the respiration components were affected by water addition. Warming increased annual R_h by 62% but had no effect on R_a. Overall, warming did not significantly increase annual R_s. Warming showed a stronger impact on R_s in the non-growing season but had a smaller impact in the growing season. Warming increased R_a in the non-growing season but decreased it in the growing season. The effects of warming on R_h were similar for the two periods. Our results highlight the differential response of R_a and R_h to warming, which was mediated by water addition or season. For this and other similar forest sites that don't experience water limitation, global warming may have a positive feedback on atmospheric CO_2 concentrations through enhanced soil respiration.

1. Introduction

Tropospheric concentrations of carbon dioxide (CO_2) and other trace gases have been increasing since the beginning of the Industrial Revolution, with an even more rapid increase over the last 50 years (IPCC, 2013) and this has been closely linked to climate warming (Crowley, 2000). It has been predicted that this increase in greenhouse gases will raise the mean global air temperature by 1.1–6.4 °C by the end of this century, with an increased warming rate occurring in Europe (IPCC, 2013). Soil respiration (soil surface CO_2 flux, R_s) is the second largest carbon flux (60–80 Pg C yr^{-1}) in the terrestrial carbon cycle (Davidson et al., 2002) and comprises 20–40% of the carbon (C) exchange to the atmosphere. Previous global warming manipulation experiments, conducted during the last two decades, have reported a stimulation of R_s and an increase in the flux of C from the soil to the atmosphere (Rustad et al., 2001; Wu et al., 2011). For example, an increase of 1 °C in air temperature could cause a 10–28% greater C release (11–34 Pg C yr^{-1}) due to increased soil respiration (Schimel et al., 1994). An increase in R_s could weaken the C sink strength of terrestrial ecosystems and even turn them into C sources (Canadell et al., 2007; Cox et al., 2000; Jones and Huntingford, 2003). Forest soils in the northern hemisphere in particular, constitute an important terrestrial C sink (Goodale et al., 2002; Janssens et al., 2003). Therefore, even small increases in C emissions induced by climate change for these forest soils could lead to large global increases in atmospheric CO_2 concentrations.

As one of the main environmental factors driving R_s, soil temperature controls and regulates a range of biogeochemical processes that determine the cycling of C (Flanagan et al., 2013). R_s is also affected by water availability and generally increases with an increase in SWC at the lower range of values for SWC, but can decrease at higher values (Davidson et al., 1998; Deng et al., 2012; Hui and Luo, 2004; Linn and

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Doran, 1984). Nevertheless, the nature of the impact of soil temperature in combination with other environmental factors, such as water availability, on R_s can be highly variable (Fernandez et al., 2006; Jenkinson et al., 1991). Reductions in R_s have been reported in drier ecosystems where moisture deficits were increased by warming, whilst increases have been reported in ecosystems with higher water availability. Therefore, the response of R_s to elevated temperature in individual studies may vary from an increase in emissions (Lin et al., 2011; Melillo et al., 2017; Noh et al., 2016; Schindlbacher et al., 2009; Wan et al., 2007; Zhou et al., 2006), no effect (De Boeck et al., 2007; Li et al., 2013) or even reduced emissions (Liu et al., 2009; Pajari, 1995; Saleska et al., 1999; Verburg et al., 2005). Generally, fewer warming studies on soil respiration have been carried out in temperate forest ecosystems where water availability is less constrained, with the nature of the impact of elevated temperature remaining uncertain.

As the primary pathway for the return of soil C to the atmosphere, a better understanding of R_s, and its components, as well as their response to a changing climate is important to assess the future ecosystem C balance. Total soil respiration comprises two major source components: an autotrophic component (R_a), originating from the respiratory activity of roots and the associated rhizosphere, and a heterotrophic component (R_h), arising from microbe-associated soil organic matter (SOM) decomposition (Hanson et al., 2000; Kuzyakov, 2006; Subke et al., 2006). The important distinction between R_a and R_h is that the former largely represents the respiration of C recently assimilated by plants, whereas the latter releases C that may have had up to millennial residence times in the soil (Trumbore, 2000). In studies conducted in temperate coniferous forests, R_h and R_a responded similarly to increasing temperatures (Schindlbacher et al., 2009; Vogel et al., 2014. In contrast, Zhou et al. (2010) reported a negative effect of warming on both R_h and R_a. In a recent report of a long-term warming study on a mixed hardwood forest stand, most of the warming-induced increase (66%) in R_s was due to an increase in R_h, with a smaller effect (33%) on R_a (Melillo et al., 2017). As the experimental conditions may have a large impact on the responses of the soil C cycle to warming, as well as ongoing uncertainties about how warming affects R_h and R_a in different ecosystems, more information is required to obtain a better understanding of how increased temperatures affect the soil C balance.

Terrestrial C cycle feedbacks to climate warming can vary strongly with precipitation, which is projected to increase at high latitudes and decrease in most subtropical regions (IPCC, 2013). The combined effects of warming and altered precipitation are expected to have strong influences on the C balance. For example, a combination of warming and decreased precipitation can cause large C losses (Angert et al., 2005; Breshears et al., 2005; Ciais et al., 2005; Loik et al., 2004). In contrast, decreased water availability could also diminish or even inhibit any warming-induced stimulation of R_s (Liu et al., 2009; Schindlbacher et al., 2009; Suseela and Dukes, 2013; Wang et al., 2014). Divergent results have also been reported from experimental manipulations of the effect of precipitation/water addition on R_s (Jia et al., 2014; Liu et al., 2015; Wan et al., 2007; Wei et al., 2016), and few studies have quantified the responses of R_h and R_a in response to warming in combination with differences in soil moisture (Suseela et al., 2012). Therefore, it remains unclear whether or not R_s and its components respond in a similar manner to simultaneous warming and altered precipitation.

In this study, we investigated the impacts of soil warming and water addition, as well as their interaction, on R_s and its components, R_a and R_h. Such multifactor experiments are important to improve the predictive ability of multifactor climate models, as single factor experiments may fail to account for the interactive effects of different climate change drivers (Leuzinger et al., 2011; Norby and Luo, 2004). Likewise, partitioning the autotrophic and heterotrophic components of R_s can lead to a greater mechanistic understanding of the response of R_s to environmental factors (Chen et al., 2011). This study reports on measurements made in a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) forest stand in central Ireland. These plantations are of significant commercial benefit and are considered a critical store of C in Ireland and elsewhere, a role that could be developed more extensively to further offset national greenhouse gas emissions (DAFM, 2012). Soil respiration and R_h were measured in forest plots over a period of 24 months, where the major objective was to compare seasonal variations in R_s and its components in response to atmospheric warming and how this is further impacted by alterations in water availability.

2. Materials and methods

2.1. Experimental site

The field study area was located in Dooary Forest, Co. Laois, central Ireland (52°57′N, 7°15′W; altitude of 260 m). The 30-year (1978–2007) mean annual temperature and precipitation at this site were 9.9 °C and 857 mm, with a climate typical of the northern temperate zone. Mean monthly air temperatures range from 13 to 16 °C during summer, 4–6 °C during winter, and 7–12 °C during spring and autumn. Precipitation is quite evenly distributed over the year with slightly higher rainfall during winter. The commercial management of the forest is under the control of Coillte, a semi-state forestry company and the measurement plots were located in a Sitka spruce first rotation stand planted in 1988 on previously unmanaged grassland without fertilization, at a planting density of 2300 stems ha^{-1}. The size of the forest stand covers a total area of 42 ha. The measurements for this investigation were conducted in close proximity to an eddy covariance tower used for long-term (2002-present) measurements of C fluxes, with available biomass and climatic data, which have been used as part of a long-term forest C sequestration and greenhouse gas emissions monitoring site. Shallow drains were created to improve soil drainage prior to forest establishment in 1988 and trees planted on a 2 m by 2 m grid. The dominant soil type in the area is a wet mineral soil classified as low humic surface-water gley. The main soil properties for this site are detailed in Table 1. The forest stand has been thinned four times, in 2006, 2008, 2012 and 2015 resulting in a more open canopy. Little understory vegetation was present except some moss and fungi. However, some herbaceous vegetation was present in the thinning lines where trees were removed and the forest floor was open to receive radiation and rainfall directly. Other biometric and micrometeorological information can be found in Saunders et al. (2012, 2014).

2.2. Experimental design

The experiment used a paired nested design with warming as the main factor and watering as a secondary factor. Infra-red (IR) heaters were used in this study in order to simulate warming in a comparable way to the way that GHGs warm the earth surface through their influence on the downward infra-red flux (Aronson and McNulty, 2009). Whilst the disadvantage of this approach is that the air underneath the heaters is drier compared to the control, reducing the relative humidity

Table 1
Soil properties at the forest site. Values are mean (SE). BD, bulk density; STC, soil total carbon; STN, soil total nitrogen; NH_4^+, ammonium; NO_3^-, nitrate.

Variables	Unit	Mean	SE
BD	g cm^{-3}	0.83	(0.04)
STC	%	4.22	(0.58)
STN	%	0.27	(0.01)
NH_4^+	mg kg^{-1} soil	6.51	(0.83)
NO_3^-	mg kg^{-1} soil	2.51	(1.06)
pH	–	3.90	(0.12)
Sand	%	9	(2.0)
Silt	%	38	(0.9)
Clay	%	53	(1.8)

(Amthor et al., 2010; Aronson and McNulty, 2010), the wind speed and light levels remain largely unaffected and their deployment causes minimum disturbance, unlike the use of electrical cables. Heating associated water losses can also be compensated by using supplementary additions of water.

Pairs of 2 × 2 m plots in the forest were replicated three times. One plot was warmed continuously using IR heaters (165 × 15 cm, MSR-2420, Kalglo Electronics Inc., Bethlehem, PA, USA) from 18 December 2013 and the other was included as a control, and exposed to ambient conditions. One IR heater was suspended 1.2 m above the ground in each warmed plot. The heaters were set at outputs of approximately 1000 W to heat the warmed plots continuously 24 h daily. In the control plot, one 'dummy' heater made of aluminium with the same shape and size as the IR heater was suspended at the same height to simulate any shading effects of the heater. For each paired plot, the distance between the control and the warmed plot was at least 5 m to avoid indirect heating. Each 2 × 2 m plot was then divided into two 2 × 1 m subplots. In order to prevent lateral movement of water/nutrients, each plot was divided across the middle by a 2-m long PVC sheet inserted approximately 10 cm into the soil (Xu and Luo, 2012). One subplot in each warmed plot was watered to assess the effects of warming-related water deficits resulting in four treatments, control (C), warming (W), water addition (P), and warming plus water addition (WP). The full experimental treatments are also listed in table S3 of the supplementary information.

Water additions, to replace any warming-associated losses, were applied evenly with a watering can equipped with a fine rose sprinkler approximately twice a month over the growing season from May to October. A full year has been divided into a non-growing season and growing season based on the ambient air temperatures at our site. During the non-growing season, daily mean soil temperatures were generally below 10 °C, while they were above 10 °C during the growing season. Based on continuous monitoring of soil moisture from November 2013 to March 2014, before the respiration measurements started in March 2014, warming in this study caused a reduction in soil moisture by approximately 5%. During the summer months, the water deficit associated with experimental warming could be even larger, therefore in order to ensure the adequate compensation of water losses, each watered plot received 170 mm of water in total every year during the growing season in both 2014 and 2015, which represented approximately 20% of the annual precipitation for this region. Due to the consistently high water table at this site, the leaching of N caused by additional water can be ignored. Water additions were initiated in May 2014.

2.3. Measurement of soil respiration and its components

A PVC collar (200 cm^2 in area, 16 cm in diameter, and 5 cm in height) was inserted approximately 3 cm into the soil in December 2013 at the center of each plot, for measuring R_s. Small living plants were removed at the soil surface at least one day before the R_s measurement to eliminate the effect of above-ground biomass on soil respiration (Zhou et al., 2007). A deep PVC pipe (200 cm^2 in area and 35 cm in depth) was inserted into the soil in order to exclude roots in each plot near the shallow collar in July 2014 for subsequent measurement of R_h. In this study, measurements of R_h were delayed for 6 months to ensure the re-stabilization of soil conditions and the death of living roots within the exclusion pipes, and to reduce disturbance effects associated with the installation of the pipes. Measurements of soil respiration (R_s and R_h) were made approximately twice a week between 10 a.m. to 3 pm (local time), using a 1412 Photoacoustic Field Gas Monitor (PAS, INNOVA Air Tech Instruments, Ballerup, Denmark). R_a was calculated as the difference between R_s measured from the shallower soil pipes and R_h measured from the deeper soil pipes. Adjacent to each soil respiration measurement, soil temperature and soil water content at 5 cm depth were measured using a WET sensor (Delta-T Devices Ltd., Cambridge, UK).

2.4. Measurement of tree growth

The growth of trees was monitored using continuous measurements (n = 3) of radial increment using point dendrometer sensors (ZN11-T-WP, Natkon.ch, Hombrechtikon, Switzerland) from November 2014 in the warmed and control plots. The dendrometer sensor was located against the tree stem at a height of 1.3 m above the soil surface. Measurements were taken every minute and stored as 10-min means using a CR1000 data-logger (Campbell Scientific Inc., UK). The estimation of annual radial growth of trees was made using the maximum daily values (Bouriaud et al., 2005).

2.5. Determination of litter decomposition rates

Litter decomposition rates were determined using the litter bag method described by Robertson (1999). Sitka spruce litter samples from the forest were collected in October 2013, and then weighed (after drying at 65 °C for 48 h) into litterbags (approximately 8 × 8 cm dimension) made of polyester curtain netting with a mesh size of 0.2 × 0.6 mm. This mesh size should allow most fungi, bacteria and soil organisms to colonize the litter materials but exclude larger organisms such as isopods and earthworms. All the bags were sown together using nylon thread. The bags were filled with between 2.5 g and 9.0 g of plant material and the initial weights recorded. On 18th December 2013, ten litter bags were placed on the soil surface of each of the three forest plots. The litter bags were anchored to the soil with iron wire to ensure firm contact with the surface. A total of 120 bags were used in the study (4 treatments × 3 plots × 10 bags). Six litter bags were sampled (collected) approximately every two months from each treatment between 18/12/2013 and 5/12/2014. After the litter bags were collected, they were gently scraped to remove surface debris, dried at 65 °C for 48 h, and then brushed lightly to remove remaining debris. The dry mass of the contents of each litter-bag was then measured.

2.6. Soil analysis

Soil samples were collected in September 2014, February 2015, June 2015, July 2015, August 2015, and October 2015 for determination of soil properties and in August 2015 and December 2015 for microbial biomass determinations. Two cores (3 cm diameter, 10 cm deep) from the upper soil layers were taken randomly from each plot in close proximity to each chamber and mixed well to produce one composite sample. Each composite sample was passed through a sieve (4 mm diameter), and any visible living plant material was removed manually from the sieved soil. The sieved soil was kept in a cold room at 4 °C prior to the analysis of dissolved C and N concentrations and microbial biomass C and N. A subsample of each soil was air-dried and ground (< 250 μm) prior to further physical and chemical analysis.

Total soil C and N concentrations were measured on 0.1 g soil samples previously air dried and ground, using a CHN (carbon, hydrogen, nitrogen) analyser (TrueSpec®, Leco Corporation, St. Joseph, USA). Soil mineral N, ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were determined on 5 g samples of fresh soil using a 2 M KCl solution extraction procedure and measured using a nutrient analyser (Lachat Quickchem®, 5600 Lindbergh Drive, Loveland, Colorado, USA). The same extracts were used to determine dissolved C and N concentrations with a TOC/TN analyser (TOC-V Shimadzu Corp. Tokyo, Japan). Soil pH was measured using water extracts at a 1:2.5 dry soil/water ratio with a pH meter/probe (Thermo Fisher Scientific Inc., Waltham, Michigan, USA). The C and N concentrations in K_2SO_4 extracts of fumigated and non-fumigated soils were measured using the TOC/TN analyzer and MBC and MBN concentrations calculated by the differences between fumigated and non-fumigated samples divided by a factor of 0.45 (Wu et al., 1990).

2.7. Data analysis

The relationships between R_s (μmol m^{-2} s^{-1}) and soil temperature (T, °C) was analyzed using the following exponential model:

$$R_s = a \exp^{bT} \quad (1)$$

Where the coefficient a is the value of R_s at 0 °C, and coefficient b is the sensitivity of R_s to T.

The temperature sensitivity of R_s (Q_{10}), which is the relative increase in R_s for a 10 °C increase in T, for each treatment, was calculated using coefficient b:

$$Q_{10} = \exp^{10b} \quad (2)$$

Where b is the regression coefficient in Eq. (1).

The relationship between R_s (μmol m^{-2} s^{-1}) and soil water content (θ, % v/v) was analyzed using a linear model:

$$R_s = c\theta + d \quad (3)$$

Where c, d are linear regression coefficients.

To assess the warming effects on the measured CO_2 fluxes, the relative warming effect sizes (ES, %) were described as percentages using the following equation:

$$ES = \frac{R_w - R_c}{R_c} \times 100 \quad (4)$$

Where R_w and R_c are the mean respiration rates in the warmed and control plots, respectively.

Specific decomposition rates (k) were determined by fitting an exponential function to data of the mass remaining after decomposition time (Olson, 1963) as:

$$\ln(\frac{M_t}{M_0}) = -kt + c \quad (5)$$

Where M_t is the mass remaining at time t, M_0 is the initial mass, t is the time in years, k is the decay constant, c is the intercept of the regression. This model was used to calculate one specific decomposition rate, k, for each species under each treatment.

Cumulative soil respiration for each treatment was calculated by summing the products of soil respiration and the number of days between measurements (Benanti et al., 2014; Zhou et al., 2007). Analysis of variance (ANOVA) of data from the split-plot design was used to examine the effects of warming and water addition, and their interactions on soil temperature, soil moisture, and soil respiration parameters (R_s, R_h, R_a, and R_h/R_s). A general linear model (GLM) was used to test treatment effects on litter decomposition rates, tree annual stem increment, soil temperature and soil moisture. The effects were considered to be significantly different if $P < 0.05$. Comparisons of means were further carried out using Tukeys post-hoc test if the effects of treatments are statistically significant. Regression analysis was used to investigate relationships among soil respiration parameters, soil temperature and soil water content. All these statistical analyses were performed using SAS software v9.3 (SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Impact of soil warming and water addition on soil respiration and related parameters

Warming significantly ($P < 0.05$) increased the mean soil temperature by 1.9 ± 0.5 °C over the warming period. Warming was slightly unequally distributed and amounted to an increase of 1.6 ± 0.4 °C during the growing season (April–September) and 2.3 ± 0.4 °C during the non-growing period (October-March) (Fig. 1a). In contrast, warming significantly ($P < 0.05$) reduced the mean soil moisture content by ~4.1% over the whole warming period; by ~4.3% over the growing season and by ~3.8% over the non-growing season

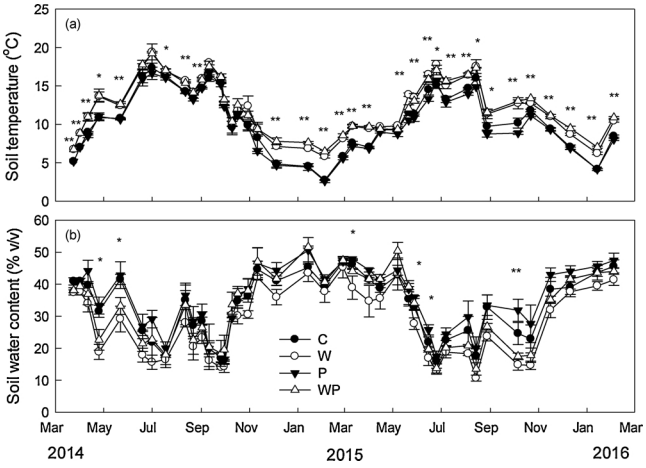

Fig. 1. Seasonal variations in soil temperature (T, a) and soil moisture (M, b) at a depth of 5 cm. Water addition was applied approximately twice a month from May to October every year in 2014 and 2015. Vertical bars represent the standard error of the mean (n = 3), * $P < 0.05$; ** $P < 0.01$ indicating significant differences between the four treatments. C, control; W, warming; P, water addition; WP, warming + water addition.

(Fig. 1, Table S2). However, significant effects of warming on soil moisture were only found on a few dates (Fig. 1b).

Total soil respiration varied seasonally as did R_h and R_a, although data was only available to compare R_h and R_a in 2015/2016, with somewhat higher values for R_s in 2015/2016 compared with 2014/2015 (Fig. 2, Table S2). Over the two consecutive years, the mean R_s, R_h, and R_a values in the control treatment were 1.62 ± 0.13, 0.54 ± 0.07, and 1.04 ± 0.17 μmol CO_2 m^{-2} s^{-1}, respectively. The mean R_s, R_h, and R_a values in the warming (W) plots were 1.92 ± 0.15, 0.99 ± 0.14, and 0.98 ± 0.13 μmol CO_2 m^{-2} s^{-1}, respectively, over the whole study period. Mean values for R_s, R_h, and R_a in the control during the growing season were 2.08 ± 0.08, 0.71 ± 0.07, and 1.57 ± 0.14 μmol CO_2 m^{-2} s^{-1}, respectively, while during the non-

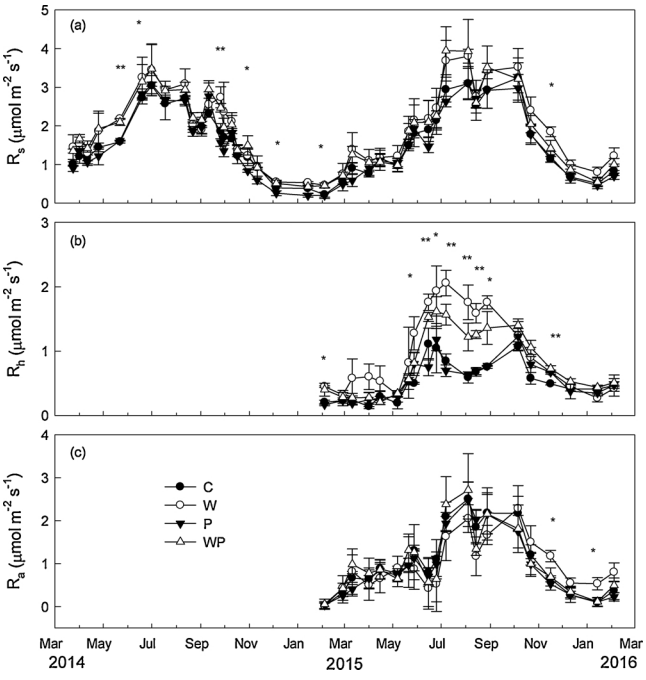

Fig. 2. Seasonal variations in total soil respiration, R_s (a), heterotrophic respiration, R_h (b), and autotrophic respiration, R_a (c). See Fig. 1 for abbreviations.

Table 2
Statistical significance (P values) of the ANOVA for the effects of warming (W) and watering (P), and their interactions with the different variables. Significant difference is highlighted in bold (P < 0.05); Df = degrees of freedom.

Factor	Df	T	M	R_s	R_h	R_a	R_h/R_s	Q_{10}_R_s	Q_{10}_R_h	Q_{10}_R_a
Warming (W)	1	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	0.973	**0.017**	0.348	**0.025**	0.082
Watering (P)	1	0.592	**< 0.001**	0.302	0.208	0.700	0.940	0.346	0.230	0.074
W × P	1	0.660	0.494	0.892	**0.020**	0.461	0.151	0.347	0.376	0.629

growing season, these were 0.84 ± 0.06, 0.30 ± 0.03, and 0.46 ± 0.07 μmol CO_2 m^{-2} s^{-1}, respectively (Fig. 2, Table S2).

There were significant warming effects on soil temperature, soil moisture, heterotrophic respiration (R_h), total soil respiration (R_s) and the ratio, R_h/R_s, although there were no effects on R_a. Watering only significantly affected the soil moisture content and the only significant interactive effect of warming and watering was on R_h (Table 2). On average, R_s and R_h were increased by 23% and 66%, respectively, due to experimental warming over the course of the experiment, regardless of water addition (P < 0.001). The proportional contribution of R_h to R_s was increased by 23%, on average, by warming (P = 0.017, Table 2).

The warming effect on R_s and R_a was also significantly affected by season (P < 0.05) with a lower effect in the growing season and a higher impact in the non-growing season. Warming decreased R_a in the growing season, but increased it in the non-growing season. For R_h, the impact was independent of season and warming stimulated R_h to the same extent during both the growing and non-growing season (Fig. 3).

3.2. Cumulative soil respiration and its component sources

Cumulative soil respiration during the whole year (P = 0.11), the growing season (P = 0.19) and the non-growing season (P < 0.05) of 2015 were marginally greater in the warmed plots than in the control. However, heterotrophic respiration was significantly (P < 0.05) increased by warming during all three periods. The annual autotrophic respiration was unchanged by warming, due to the contrasting effects of warming during the growing season and the non-growing season. Water addition had no effects on cumulative values of R_s, R_h and R_a either annually or seasonally (Fig. 4).

The cumulative R_s, R_h, and R_a stimulated by warming during the non-growing season were 49.0 ± 18.2, 23.9 ± 10.5, 31.6 ± 20.0 g C m^{-2}, respectively. Warming also stimulated the cumulative R_s and R_h during the growing season, with maximum values of 80.6 ± 55.5 and 107.5 ± 24.0 g C m^{-2}, respectively. But warming reduced the cumulative R_a during the growing season by up to 27.0 ± 31.6 g C m^{-2}.

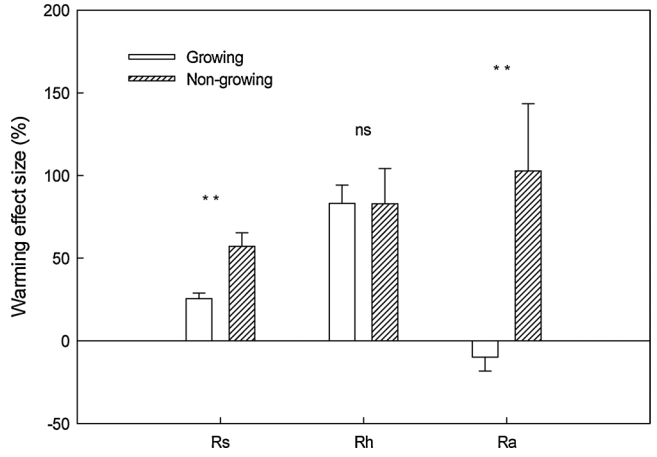

Fig. 3. Seasonal variations in the effect (%) of soil warming on R_s, R_h, and R_a. Vertical bars represent the standard error of the mean (n = 3). Results are reported for the ANOVA with season. Values labelled with an asterisk are statistically significant (** P < 0.01; ns = not significant at P < 0.05).

Thus the 23% increase in annual R_s was mainly a result of the 62% increase in annual R_h. However, the absence of an R_s response to warming during the growing season was due to compensatory effects of warming on R_h and R_a, whilst the strong response of R_s to warming during the non-growing season was due to a similar effect of warming on both R_h and R_a.

3.3. Influence on soil properties and microbial biomass

Most of the measured soil variables, except DTC and DOC were not significantly influenced by warming or watering (Fig. 5). However, there were generally higher values for the organic carbon and nitrogen compounds in the warming treatments, which were not watered. In contrast, values for microbial biomass carbon and nitrogen were reduced with warming (Fig. 5). For the organic C and N compounds, there was no evidence of any increase when watering was combined with warming, suggesting that no effects were mediated by warming-related decreases in soil moisture. However, microbial biomass C and N were unaffected by watering (Fig. 5).

3.4. The relationship between soil respiration and soil temperature and moisture content

Seasonal variations in R_s, R_h and R_a were positively correlated with temperature and inversely correlated with soil moisture. The relationship between R_a, R_s and R_h and soil temperature for both the control and warming treatments throughout the experimental period was best described by an exponential regression equation (Fig. 6). In contrast, the relationship between R_a, R_s and R_h and soil moisture was best described by a linear regression (Fig. 7). Soil temperature accounted for 69–76% of the variation in R_s, 51–71% of that in R_h, and 25–63% of that in R_a (Fig. 6, Table S1), whilst soil moisture explained 51–66% of the variation in R_s, 58–87% in R_h, and 30–47% in R_a (Fig. 7, Table S1).

Including both soil temperature and moisture in the regression models had little or only a very small impact on the explanatory power, but resulted in a slightly closer relationship with R_h (3–11%), compared to R_s (0–2%) or R_a (2–7%) (Table S1). Differences in the coefficients of determination of the exponential regressions suggested that the components of soil respiration had a different dependence on temperature. In warmed plots, there was a lower dependence of R_s and R_a on temperature, while R_h had a higher dependence on temperature (Fig. 6, Table S1).

3.5. Temperature sensitivity

To determine if warming influenced the sensitivity of the different soil respiration components to temperature, we calculated the basal CO_2 efflux (R_0) and temperature sensitivity (Q_{10}) for the four treatments using the exponential function described in Eq. (2).

Warming marginally reduced the temperature sensitivity of R_s (P = 0.348) and R_a (P = 0.082), but significantly increased it for R_h (P = 0.025). Water addition tended to increase the Q_{10} values for soil respiration and its components, R_a and R_h but this was not significant. The temperature sensitivity of R_a was the highest, with an average Q_{10} value of 5.18, followed by R_s, 4.96, and R_h, 4.44 (Table S2).

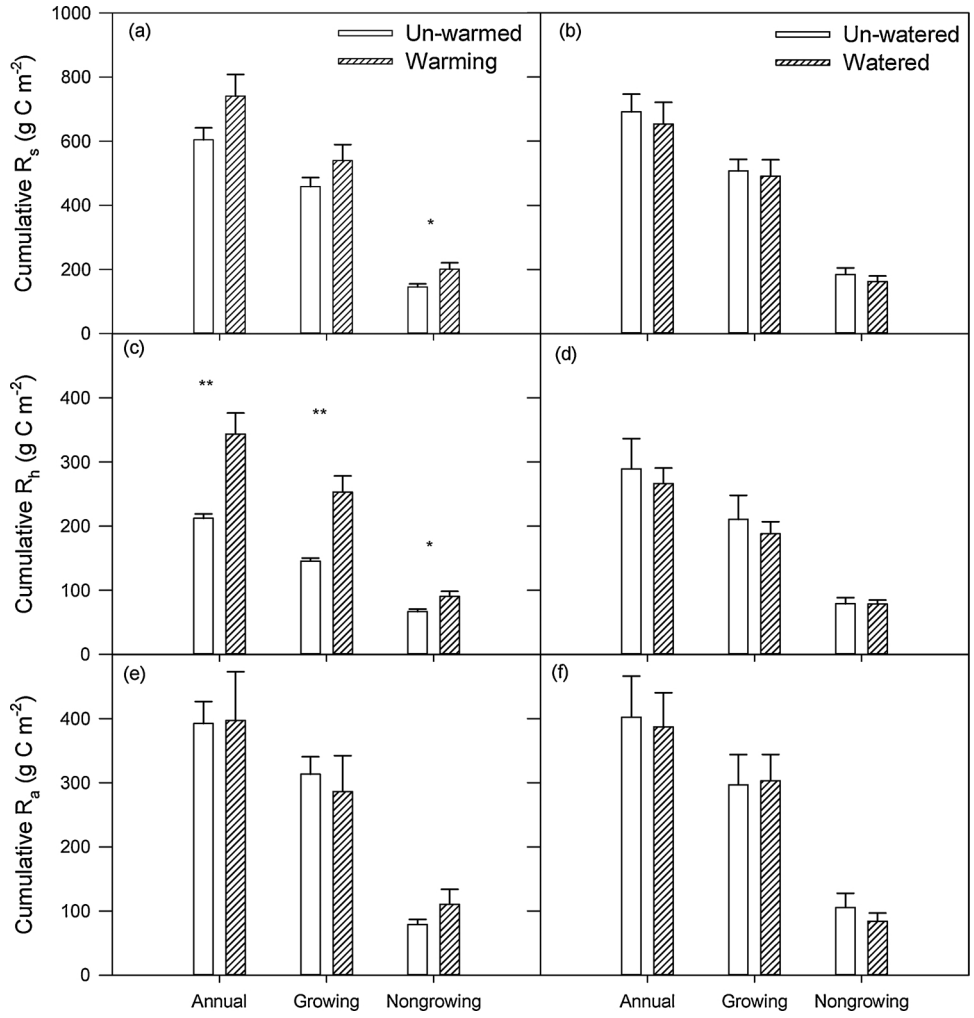

Fig. 4. Main effects of warming and watering on total soil respiration (a, b), heterotrophic respiration (c, d) and autotrophic respiration (e, f) in 2015. The panels on the left show warming effects and those on the right show watering effects. ** and * indicate the significance level at $P < 0.01$ and 0.05, respectively.

3.6. Impact on litter decomposition

The litter decomposition rates differed among treatments but followed a similar pattern throughout the experimental period (Fig. 8). An exponential model of decomposition was fitted to the experimental data and the annual decomposition rate coefficients (k) were 0.32, 0.36, 0.35 and 0.39 for the C, W, P, and WP, treatments, respectively. Warming tended to increase the decomposition rates and water addition enhanced this impact, however, the overall treatment effects were not statistically significant ($P > 0.05$) compared to the control. Warming and water addition separately seemed to have a similar effect with comparable k values for W and P.

3.7. Warming effects on tree growth

The annual radial stem increment of trees grown under ambient and warming conditions was similar and exhibited a marked seasonal pattern, with a major increase from April to September and little change for the rest of the year (Fig. 9a). The average annual radial stem increment of trees subjected to the warming treatments was not statistically different ($P > 0.05$) from trees grown under ambient conditions (Fig. 9b).

4. Discussion

4.1. Partitioning of soil respiration and its components

The average soil respiration rate measured in the control plots over the course of this study was 1.62 ± 0.13 μmol CO_2 m^{-2} s^{-1}, a value that falls well within the range (1.1–2.6 μmol CO_2 m^{-2} s^{-1}) reported for many temperate coniferous forests (Bergner et al., 2004; Curiel Yuste et al., 2004; Olajuyigbe et al., 2012; Saiz et al., 2006a). The relative contribution (40%) of R_h to R_s for control plots agreed well with results from a similar Sitka Spruce forest stand close to the study area, where R_h contributed 43–47% of R_s annually (Saiz et al., 2006a, b) and within the range of values reported for temperate deciduous forests in general, where R_h contributed 29–96% of R_s (Subke et al., 2006).

In this study, a deep-collar insertion method was used to partition R_h from R_s, which is very easy and cheap to implement. This method is among the three primary methods most widely used to partition soil respiration (Hanson et al., 2000). According to a recent meta-analysis by Wang et al. (2014), different partition methods were found to have no significant effects on R_h and R_a measurements. Nevertheless, it should be noted that some potential problems may result from the use of this method, including changes in soil moisture, only partial decomposition of roots, and alterations to soil microbial communities (Díaz-Pinés et al., 2010; Hanson et al., 2000). Soil moisture and soil microbial community composition in the deep collars (35 cm) were not measured in our study. Root exclusion methods generally result in a

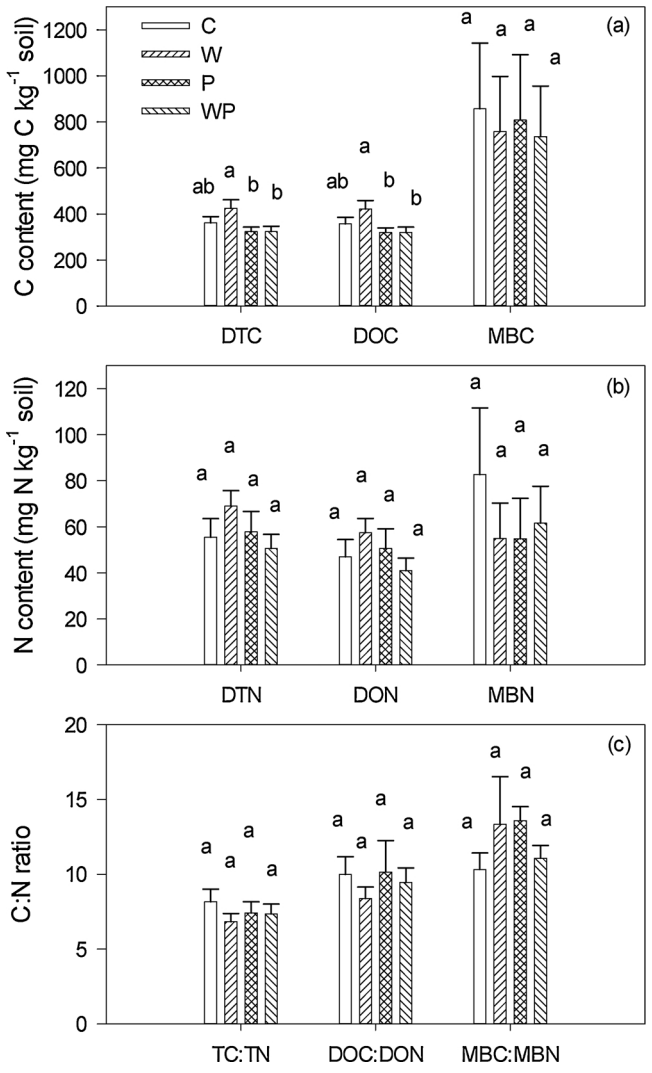

Fig. 5. Main soil biogeochemical variables by treatment. Dissolved total carbon (DTC), dissolved total nitrogen (DTN), dissolved organic carbon (DOC), dissolved organic nitrogen (DON), microbial biomass carbon (MBC), microbial biomass nitrogen (MBN). C, control; W, warming; P, water addition; WP, warming + water addition. Vertical bars represent the standard error of the means. Different lowercase letters indicate significant differences at $P < 0.05$.

transient increase of soil respiration due to decomposition of dead roots and disturbance (Hanson et al., 2000; Zhou et al., 2007), which was found to last about 5 months after collar insertion (Zhou et al., 2007). In the current study, collars were inserted into the soil more than 6 months before the measurements started in February 2015, so the effect of dead root decomposition on measured R_h should have been minimal. However, since C inputs through dead root and root exudates are excluded, we may have underestimated R_h and, in turn, overestimated R_a.

4.2. Effect of warming on soil respiration and its components

Numerous *in situ* warming manipulation studies have reported temperature-related increases in soil CO_2 emissions (Rustad et al., 2001; Wang et al., 2014). To our knowledge, this is the first investigation of warming effects on soil respiration and its source components in a Sitka spruce forest plantation. The average increase in R_s due to warming (~2 °C) during the first two years (23%) in the current study was at the lower end of the range (24–76%) found in other soil warming experiments conducted in different forest ecosystems (Bronson et al., 2008; Hagedorn et al., 2010; Melillo et al., 2002; Peterjohn et al., 1994; Rustad and Fernandez, 1998; Schindlbacher et al., 2009), but was much higher than the reported 12% mean increase obtained in a recent meta-analysis, where the temperature increase was normalized to 2 °C across all biomes (Wang et al., 2014). The response strength of carbon turnover to warming was influenced by mean annual temperature (MAT) (Wang et al., 2014), with a greater response in cooler climates than in warmer climates (Koven et al., 2017). Thus, in Ireland's cool temperate forests, the larger increase in R_s due to warming was likely due to a combination of a lower MAT and a higher soil C content.

Since temperature determines the decomposition of soil organic matter, the quantity and quality of this pool are important factors in the C balance of terrestrial ecosystems subjected to a warmer climate (Cardon, 1996; Davidson and Janssens, 2006). However, no significant differences in the dissolved carbon and nitrogen pools between control and warmed plots were observed during the 2 years of measurements in this study. This was not consistent with other studies (Bradford et al., 2008; Hartley et al., 2007; Niinistö et al., 2004; Rustad et al., 2001) where decreased labile soil organic matter pools were observed under warming due to stimulated CO_2 emissions and enhanced soil organic matter oxidation. Other studies reported increased labile soil organic matter pools due to greater above- and below-ground biomass production (Belay-Tedla et al., 2009). Rudrappa et al. (2006) found that microbial C and N pools are also important labile soil C and N pools. In our experiment, neither the soil microbial C and N, nor the ratio of soil microbial C and N differed significantly between the warmed and control forest plots, which was consistent with studies conducted in arctic tundra and tallgrass prairie (Biasi et al., 2008; Zhang et al., 2008). It is possible, however, that significant changes in the microbial community would only occur after a larger increase in temperature than the ~2 degrees used in this study. In addition, soil warming did not alter tree productivity as indicated by tree radial growth measurements. The unchanged soil biogeochemistry and plant production in the present study may indicate that the period of warming (two years) was not sufficient to affect R_s through a change in carbon substrate availability. Recent results based on a long-term soil warming study indicated that structural and functional changes in the microbial community is the dominant factor controlling the decomposition of soil C under warming conditions (Melillo et al., 2017).

A few studies have examined the effects of warming on the components of soil respiration in the field (Wang et al., 2014). To our knowledge, most of the available studies have reported positive effects of warming on both R_h and R_a (Noh et al., 2016; Schindlbacher et al., 2008; Zhou et al., 2007). However, Zhou et al. (2010) reported a warming-induced decrease of both R_h and R_a, while other studies demonstrated a warming induced increase in R_h, but a decrease in R_a (Li et al., 2013; Verburg et al., 2005). Our results showed that the stimulation of R_s by warming was mainly associated with an increase in R_h, indicating the different temperature sensitivity of R_a and R_h. In contrast, a previous study reported that soil warming stimulated R_h and R_a to a similar degree in a temperate forest (Schindlbacher et al., 2009). However, other studies found that warming induced a significant change in R_a compared to R_h, because R_a is directly related to the activities of roots and their symbionts, which depend largely on assimilate supply that may be higher when greater growth is possible (Li et al., 2013; Zhou et al., 2011). Single-factor climate change experiments have generally reported increases in soil respiration with warming. Nevertheless, we found that the effect of warming on R_s and R_a varied with season in the Dooary forest, with warming decreasing R_a during the growing season but increasing it during the non-growing season. In contrast, warming increased R_h during both the growing and non-growing seasons. The warming effect on R_s was weaker during the growing season, but was enhanced during the non-growing season. Most of soil respiration is thought to originate from near surface soil layers that would be susceptible to moisture deficits particularly in the vicinity of roots due to increased water uptake by trees. In contrast any

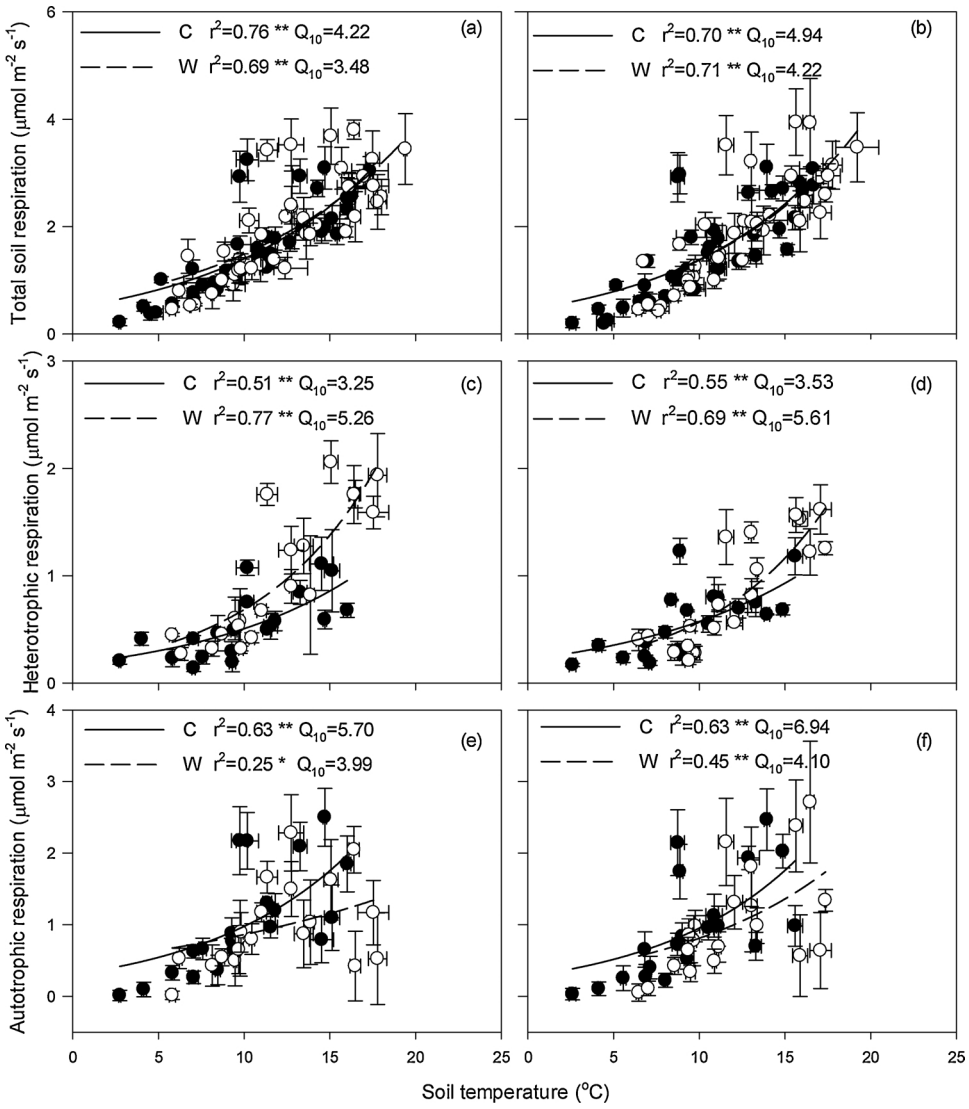

Fig. 6. Relationships between soil temperature and total soil respiration (a, b), heterotrophic respiration (c, d), and autotrophic respiration (e, f). Panels on the left show the un-watered treatments and the watered ones are shown in the panels on the right. Vertical and horizontal bars represent the standard errors of the means (n = 3). ** and * indicate the regression models are significant at $P < 0.01$ and 0.05, respectively. C, control; W, warming.

effects of moisture deficits would be expected to be less in the bulk soil (Peng et al., 2015; Suseela and Dukes, 2013). During the non-growing season, when more water was available for root and microbial activity, the warming effects on R_s were amplified by the positive feedback of elevated temperatures on R_a and R_h. Our results suggest that future warming may have a greater impact on soil respiration during the autumn/winter periods with a stronger impact on root respiration, whilst warming during the spring/summer is more likely to affect soil decomposition processes.

The warming (+2 °C) induced soil carbon loss calculated from R_h in this study was estimated to be 131 ± 27 g C m^{-2} over the one-year field investigation, which is within the range of reported values (75–180 g C m^{-2}). However, it is difficult to make direct comparison with other studies due to differences in the warming-associated temperature increases, so we normalized all the values to a 1 °C temperature increase. In the current study a 1 °C increase in soil temperature was estimated to increase annual soil carbon losses by 66 ± 14 g C m^{-2}. This increase is higher than the work of Noh et al. (2016) conducted in a deciduous cool temperate broadleaf forest as well as in the study of Schindlbacher et al. (2009) conducted in a mature boreal forest dominated by Norway spruce, both of which showed a similar stimulation of soil carbon loss by warming of 45 g C m^{-2} per year per °C temperature increase. But the increase found in the current study is much lower than the warming induced soil carbon loss of 242 g C m^{-2} per year per °C temperature increase reported by Aguilos et al. (2011) in a cool-temperate mixed forest with peat soil. However, a recent analysis from a long-term soil warming (+5 °C) study in Harvard Forest (1991–2016) by Melillo et al. (2017) reported that soil warming could result in a soil carbon loss of as much as 20 g C m^{-2} per year per °C soil temperature increase during the phase when there was a significant response of soil respiration to warming. However, there were also periods when there were no detectable losses as soil respiration in warmed plots were equal to or less than those in the control plots (Melillo et al., 2017). This indicates that there is still significant uncertainty about the influence of elevated temperatures on long term soil C losses. Warming typically raises the metabolic rates of both plants and microbes, as indicated by most greenhouse and incubation experiments. The higher R_h under warming could be due to a faster litter decomposition rate and a larger microbial biomass, as reported by Lu et al. (2013) from a meta-analysis of ecosystem responses to experimental warming. In this study warming increased surface litter decomposition rates but had no effect on microbial biomass C and N, so that the warming-related enhancement of R_h may have been mainly associated with an increased litter turnover rate. Nonetheless, the reasons for these

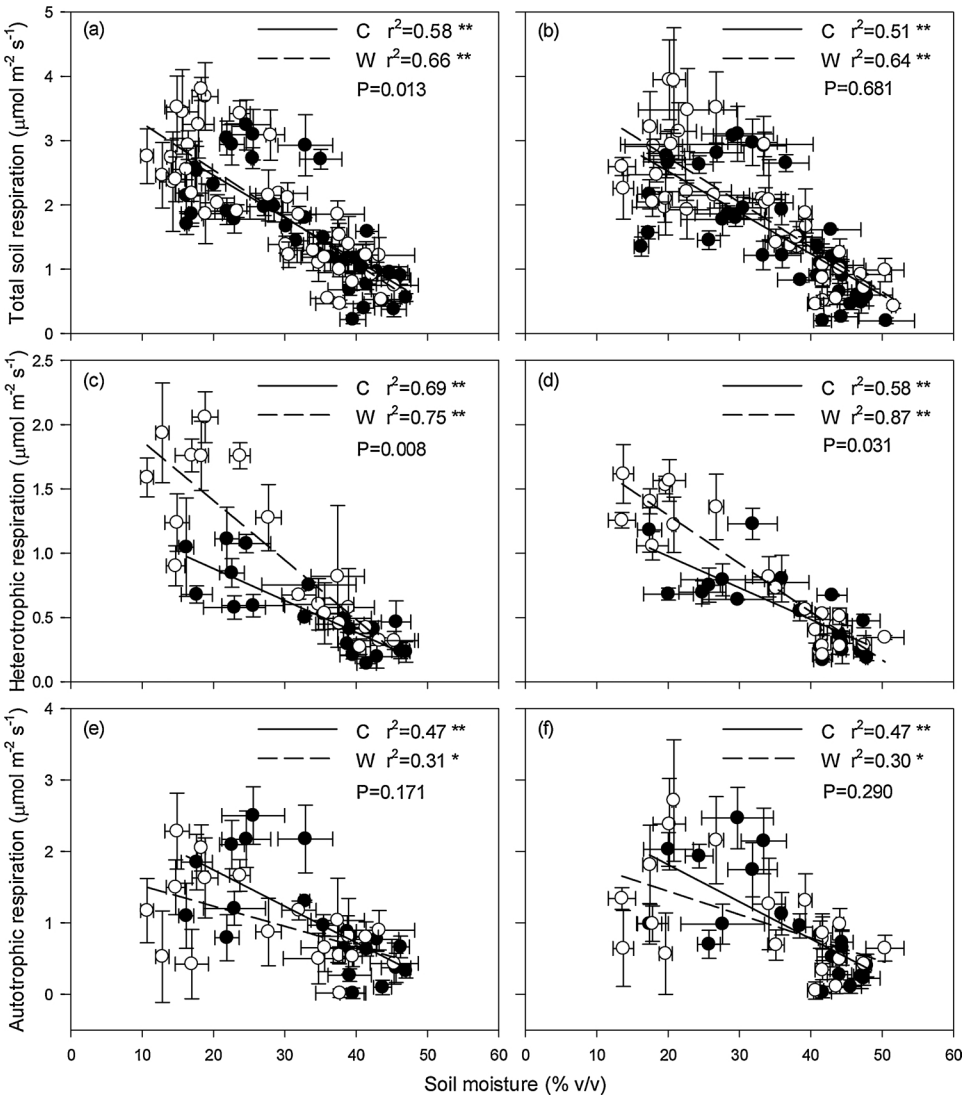

Fig. 7. Relationships between total soil respiration and soil moisture (a) and (b), heterotrophic respiration and soil moisture (c) and (d), and autotrophic respiration and soil moisture (e) and (f), in the un-watered (left) and watered (right) treatments. *P* is the probability that the slopes are the same between treatments. Vertical and horizontal bars represent the standard error of the means (n = 3). ** and * indicate the regression models are significant at P < 0.01 and 0.05, respectively. C, control; W, warming.

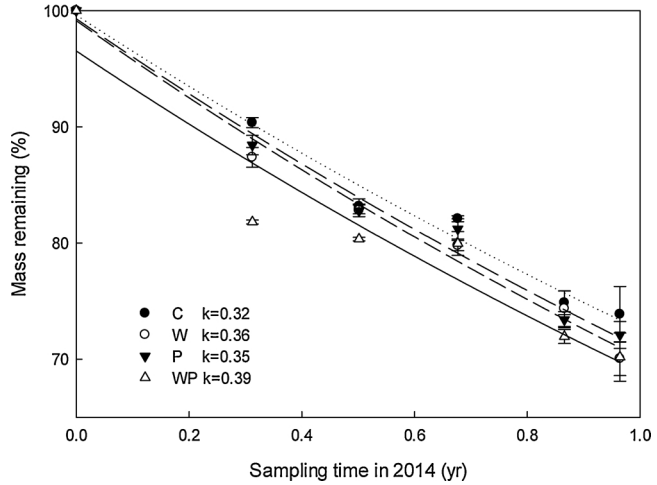

Fig. 8. Litter biomass remaining (%) and estimated annual decomposition rates (k, g g^{-1} yr^{-1}) of litter from the different treatments. Vertical bars represent the standard error of the mean (n = 3). See Fig. 1 for abbreviations.

differences are not well known, and they could be related to differences in climate, vegetation or soil characteristics, making generalizations about the effects of warming, even for similar ecosystems, difficult.

In contrast to R_h, elevated temperature (~2 °C) did not lead to significant changes in R_a. This contrasts with a study conducted in a mixed deciduous forest where R_a was decreased by a 5 °C increase in soil warming (Melillo et al., 2011), and another study conducted in a cool temperate deciduous forest, where R_a was increased by a 5 °C soil warming (Noh et al., 2016). These differences may be related to the fact that R_a is also dependent on changes in above- and below-ground productivity (Li et al., 2013; Zhou et al., 2011). R_a is related to the activities of roots and their symbionts (Hanson et al., 2000; Kuzyakov, 2006), which depend on the import of new C from the canopy. Field studies demonstrated that R_a was also significantly related to above-ground productivity (Flanagan and Johnson, 2005; Högberg et al., 2001; Yan et al., 2010). Radial growth of trees continuously monitored with dendrometers showed that warming had no effects on tree growth in the current study, supporting the proposal that unchanged R_a was caused by the lack of any warming-induced increase in plant productivity. The absence of a warming effect on tree growth may due to a number of reasons. Firstly, we warmed the forest soil but not the entire

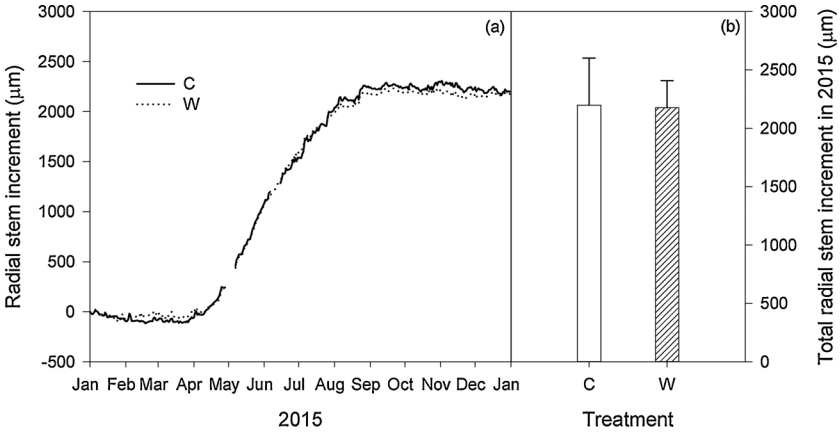

Fig. 9. Seasonal radial stem increment (a, n = 3) of trees grown under ambient soil temperatures (C), and those associated with experimental warming (W) from 1 January 2015 to December 31, 2015, and total radial stem increment in 2015 (b) of trees associated with ambient and warmed conditions. Vertical bars (b) represent the standard error of the mean (n = 3). No significant difference was found between the two treatments.

trees, thus warming may have had a negligible effect on photosynthesis and productivity. In addition, not all the root system was exposed to elevated temperatures, as the experimental plots did not encompass all the tree roots. It appears, therefore, that any modifications in autotrophic respiration may be dependent on how warming affects plant productivity. The absence of any effect of warming on tree growth could be important at the ecosystem level as any soil-associated emissions of CO_2 would not be compensated by an increase in photosynthesis, leading to greater C losses at higher temperatures.

4.3. Litter decomposition rates

Warming tended to increase the decomposition rate but this was not statistically significant. Under field conditions, however, it is difficult to detect the specific effects of temperature on CO_2 emissions or decomposition because a number of interacting factors affect litter decomposition. Initial decomposition rates can be expected to be higher during the main growing season (Berg and McClaugherty, 2008), than those reported in the current study, as the decomposition experiments commenced in November. Therefore, the use of litter bags in field experiments may require several starting points to separate the effects of season from that of any imposed treatment. Furthermore, the decomposition process may also be influenced by water availability. For this reason, the positive effects of temperature on decomposition could be reduced during dry periods, which may explain why similar decomposition rates were found in the W and P plots, as well as the enhanced decomposition rates in the combined warming with water addition plots.

4.4. Effects of water addition

It is well-documented that both soil temperature and water availability can strongly affect soil respiration and its components in many ecosystems (Jia et al., 2014; Liu et al., 2015; Raich and Schlesinger, 1992; Rustad et al., 2001; Saiz et al., 2007; Shabaga et al., 2015). No effect of watering on soil respiration was observed in the current study, nor was there any interaction between warming and watering, consistent with the report by Zhou et al. (2006). However, other studies found that R_s was enhanced by warming in the dormant season because of higher soil water contents, whilst R_s decreased in the growing season due to associated water deficits (Reynolds et al., 2015; Suseela and Dukes, 2013). It may not be surprising, however, that water availability was not a limiting factor at this site since the soil moisture at 5 cm, even during the growing season, rarely fell below 20%. Whilst it has been suggested that global change drivers may interact, resulting in smaller responses when the environmental variables have opposing effects (Leuzinger et al., 2011), this will clearly depend on the local climatic/edaphic conditions, and suggesting that, in some cases, there may be additive effects.

4.5. Temperature sensitivity of Rs and its components

The apparent Q_{10} values for R_a were higher than those for R_h and R_s, a trend also reported by others (Boone et al., 1998; Epron et al., 1999; Jiang et al., 2005; Zhou et al., 2007). Values for Q_{10} are not directly comparable between R_a and R_s, because R_s is partially determined by R_a. The Q_{10} values (on average, 5.18 for R_a, 4.96 for R_s, and 4.44 for R_h) in the Sitka spruce forest, were quite high compared to the reported range of 1.0–5.0 found in many terrestrial ecosystems (Curiel Yuste et al., 2004; Davidson et al., 2006; Poll et al., 2013; Suseela and Dukes, 2013; Wang et al., 2014). This might be related to the location's climate, because the temperature control on soil carbon turnover has been proved to be more sensitive in cooler climates than in warmer climates (Koven et al., 2017). The higher Q_{10} values for R_a than R_h may have resulted not only from the higher sensitivity of root respiration to soil temperature, but also from seasonal variations in root biomass, which tend to be higher when the temperature is higher (Boone et al., 1998; Rey et al., 2002). The different Q_{10} values for R_a and R_h suggest that the temperature sensitivity of soil CO_2 efflux depends on the relative root contribution. If this is correct, an ecosystem in which roots contribute the largest portion of the soil CO_2 efflux would be the most sensitive to climatic warming.

5. Conclusions

In summary, results from this study in a cool temperate coniferous forest revealed that warming stimulated R_s, largely through its impact on R_h, while R_a remained largely unchanged. Water addition, in contrast, had no significant effects on R_s and its components. Interactive effects of warming and water addition were found on R_h implying that warming effects on R_h were mediated by water availability. The interactive effects of warming and season on R_a, indicates that the warming effects on R_a were also modulated by environmental factors that varied across seasons. Overall, we estimate a carbon transfer of 131 g C m^{-2} per year from forest soils to the atmosphere in response to a 2 °C warming, indicating a positive feedback effect on atmospheric CO_2 concentrations due to climate change in these ecosystems.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agrformet.2018.06.020.

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